PARASITES OF *OREOLEUCISCUS POTANINI* (CYPRINIDAE) FROM LAKES OF KHAR US NUUR NATIONAL PARK (MONGOLIA)

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Freshwater ecosystems of Mongolia belong to the three major Central Asian drainage systems: Arctic drainage, Amur River drainage, and Central Asian Internal drainage. The Great Lakes Depression takes considerable part of the latter. One of the few fish species living there, *Oreoleuciscus potanini*, is the most common and widespread endemic species in the Central Asian region. Parasitological surveys on *O. potanini* from the Great Lakes Depression have not occurred regularly in recent years. Consequently, this study was conducted to explore the species diversity of helminth parasites in *O. potanini* in the three lakes of Khar Us Nuur National Park. In total, 52 *O. potanini* specimens were collected from the lakes Khar, Khar Us and Durgen and sampled in August 2012. In addition to the parasites, the age and diet spectrum of the fish species were studied. The fish were examined for infection with ecto- and endo- macroparasites. The species composition of *Diplostomum* spp. metacercariae from the eyes of fish was investigated using a molecular approach. In the lakes Khar and Khar Us the fish age ranged from four to 32 years old and from eight to 35 years old, respectively. Fish of four age groups (9, 10, 11 and 14 years old) were in Lake Durgen. Algae and various insects, including Chironomida larvae were the main food of the *O. potanini* in all three lakes. When the diet was investigated we found that in Lake Durgen *Cladocera* crustaceans were the significant component in the fish diet, and no fish was found in the *O. potanini* diet there. During the study 26 parasites species were identified from the three lakes. The total fauna is represented by four phyla, including Acanthocephala (one species), Annelida (one species), Nematoda (four species), Platyhelminthes (20 species). The last group was the most numerous and diverse, including three species of Cestoda, six species of Monogenea and 11 species of Trematoda. Five species of parasites were specific to *O. potanini* only (monogeneans *Gyrodactylus mongolicus*, *G. oreoleucisci*, *G. pewsowi*, nematodes *Philometra oreoleucisci* and *Rhabdochona humili*). The other helminthes exhibited a low host-specificity, infecting a wide range of fishes in the Holarctic. The larvae of endohelminthes predominate in the parasite fauna. The majority of these parasites enter the fish via various invertebrate species during *O. potanini*'s feeding. Our study provided novel data on the species diversity of *Diplostomum* spp. metacercaria in *O. potanini*'s eyes. They were represented by three species: *Diplostomum spathaceum*, *D. pseudospathaceum* and *Diplostomum* sp. LIN2. The species richness and diversity of parasites were much higher for *O. potanini* from the lakes Khar and Khar Us (26 species), than that for *O. potanini* of Lake Durgen (15 species). The possible reason for the absence of some parasites in Lake Durgan is an increased water salinity. It is likely that, despite the potential for the fish to exist under conditions of an elevated salinity, parasites (or their invertebrate hosts) are not adapted to it. Our findings clarified the known parasite diversity in lakes of the Khar Us Nuur National Park, indicating that the Great Lakes Depression ecosystem may be characterised by many unique parasite assemblages. The results of investigation on the parasitic fauna of *O. potanini* confirm a review of the evolutionary youth of this fish group.

Key words: Dzabkhan River basin, endemic, fish, Great Lakes Depression, helminthes, species composition

Introduction

Monitoring studies in the Protected Area systems cover numerous biota parameters. On their basis criteria for assessing the natural environment and future trends in ecosystem change are identified. One of the biological pollution forms is «parasitic pollution», which can be defined as penetration of parasitic organisms into environment and subsequent reproduction. Parasites comprise a substantial proportion of global biodiversity and exert important ecological influences on hosts, communities and ecosystems, but our knowledge of how parasite populations respond to human impacts is in its infancy (Wood et al., 2013). In this regard, it is relevant to develop methods of parasitological research as an important diagnostic tool for biomonitoring in Protected Areas.

One of the global issues is to save biodiversity of water ecosystems with a high rate of endemism. Moreover, fish, serving as a fundamental component of any water ecosystem, represent an important resource for the economy. The specially introduced parasites are a potentially threat to fish health and population abundance. Specialisation of the parasite has been viewed as the consequence of a long-term evolutionary process, especially true in the case of isolated populations (Sasal et al., 2004).

Therefore, in different countries, research has been conducted for a long time, not only for fish, but also for their parasites in Protected Areas.

Some of the investigations concerned the parasite communities and species composition in different fish species (Mudry & Anderson, 1977; Boomker, 1994; Murcia et al., 2006; Morozińska-Gogol, 2007, 2009; Butorina et al., 2008; Shukerova & Kirin, 2008; Moravec & Bakenhaster, 2010; Sandlund et al., 2010; Shukerova et al., 2010, 2017; Sokolov & Gordeev, 2014; Chunchukova et al., 2016; Chunchukova & Kirin, 2018; Rubtsova & Kutsokon, 2018; Utevsky et al., 2018). Other studies devoted to different systematic groups include data on fish parasites in Protected Areas (Sasal et al., 2004; Galli et al., 2007; Kirjušina & Vismanis, 2007; Székely et al., 2009; Wood et al., 2013; Halajian et al., 2018; Hoogendoorn et al., 2020). Some results make it possible to describe new parasite species or revise previous data on morphology, molecular characteristics and phylogeny, host specificity of fish parasites in Protected Areas (Moravec, 2001; Székely et al., 2012; Borkhanuddin et al., 2014; Stunžėnas et al., 2014; Molnár et al., 2015; Presswell & Blasco-Costa, 2019; Scholz et al., 2019). Despite numerous publications on fish parasites in different Protected Areas of the world, no such material exists in Mongolian Protected Areas in recent years.

Mongolia is situated on the Central Asian plateau comprising not only a large arid zone, but also a number of rivers and lakes. The freshwater ecosystems of Mongolia belong to the three major Central Asian drainage systems, including Arctic, Pacific Ocean or Amur River drainage, and Central Asian Internal drainage. Their watersheds are clearly separated (Sokolov & Shatunovskiy, 1983).

In the Mongolian Central Asian Inland Basin, the fish fauna of the water bodies includes *Thymallus brevirostris* Kessler, 1879, and fishes of the genera *Orthrias* Jordan & Fowler, 1903, *Barbatula* Linck, 1933, and *Triplophysa* Rendahl, 1933. However, *Oreoleuciscus potanini* Kessler, 1879 is the most numerous and widespread fish species in the region (Dgebuadze et al., 2003, 2014, 2017; Mendsaikhan et al., 2015; Prokofiev, 2016).

Oreoleuciscus potanini is an endemic species distributed extensively throughout the Central Asian fauna. The species is characterised by an extremely high morphological diversity. According to paleontological data, the formation of the genus *Oreoleuciscus* is associated with intensive tectonic transformations in Central Asia during the Pliocene – Pleistocene. The latter caused a deep restructuring of the relief and a number of water bodies in the region, which in turn led to an extreme decline of the fish fauna diversity (Sytchevskaya, 1989). The formation of Central Asian populations took place under extremely high varying abiotic conditions. Due to fluctuating environmental conditions and with almost complete absence of competition from other fish species, *O. potanini* in Central Asia had the opportunity to adapt to a range of habitats (Dgebuadze et al., 2020). Currently this group dominates in the fish population of most water bodies in the Central Asian Inland Basin of Mongolia, gradually expanding its range to the Baikal Lake Basin (Dgebuadze et al., 2003; Slynko & Borovikova, 2012).

Oreoleuciscus potanini is a convenient fish species to study different environmental and evolutionary issues, including the parasite faunas. Since parasites co-evolve together with the hosts, information on their species composition can be useful to study as the taxonomy problems of the genus *Oreoleuciscus*, as any changes in their biology, habitat conditions, can also help to study the total dynamics of ecosystems. Information about the fish helminthes in water bodies of a unique Central Asian drainage basin, such as Khar Us Nuur National Park, would therefore offer the opportunity to use these systems as model for future studies of speciation.

The first data on fish parasites of varying geographical basins in Mongolia are fragmentary and were published a long time ago (Ergens & Dulmaa, 1970; Moravec & Ergens, 1970; Scholz & Ergens, 1990). Later papers on fish parasites in water bodies of the Central Asian drainage basin were obtained and summarised (Kazakov & Paranlejamts, 1985; Paranlejamts, 1993; Roitman et al., 1997; Pugachev, 2001, 2002, 2003, 2004; Batueva, 2011). However, recently there have been no new field-based studies carried out to examine the taxonomy and biology of both the fish hosts and parasites in this region. Due to the lack of any recent studies investigating fish parasites in the Central Asian drainage basin, a new study began in 2011 as a part of the Joint Russian-Mongolian Biological Expedition. During this period data on parasites of *Rutilus rutilus* Linnaeus, 1758, *Perca fluviatilis* Linnaeus, 1758, *Barbatula conilobus* Prokofiev, 2016 were obtained (Lebedeva et al., 2015, 2019). During the study, a new species *Gyrodactylus* was found, *Gyrodactylus albolacustris* Lumme, Ziętara & Lebedeva, 2017, being described from *Phoxinus phoxinus* Linnaeus, 1758 using data on Mongolian parasites (Lumme et al., 2017). Additionally, special attention was paid to the study of several species of helminth parasites in *O. potanini*. The morphological variability of immature *Proteocephalus torulosus* (Batsch, 1786) from *O. potanini* was studied for the first time (Anikieva et al., 2013). Finally, species composition of trematodes from eyes of different fish species were studied using a molecular genetics approach (Lebedeva et al., 2020).

The current study was devoted to helminth parasites of *O. potanini*. It represents a part of a more comprehensive investigation of the parasitic fauna of fish carried out in the three lakes of the Khar Us Nuur National Park aiming to characterise parasites as an integral part of the biodiversity in the study region.

Material and Methods

The study was conducted in August 2012 in the Khar Us Nuur National Park (Great Lakes Depression, Western Mongolia) (Fig. 1). According to the WWF recommendation to preserve the unique natural Wetlands complexes of Mongolia, the Khar Us Nuur National Park was set up in 1997. This Protected Area is located in Western Mongolia, in the Great Lakes Depression. Forming parts of this region are the Chono Kharaih River, Mongolian part of the Altai ranges, and the eastern spurs of the Jagalant Hairhan. All of them are within the bounders of the Khar Us Nuur National Park. Lakes Khar Us, Khar and Durgen belonging to the Central Asian Drainless basin form the central part of this Protected Area.

Lake Khar Us (or Black Water Lake) is of tectonic origin and located at an altitude of 1157 m a.s.l. among the mountain ranges of Altai and Hangai. Its area is more than 180 km^2, including more than 20 islands. This water body is connected by channels with the lakes Durgen and Khar (Dgebuadze et al., 2014).

Lake Khar (or Black Lake) is a freshwater lake located east of Lake Khar Us and connected to it by the channel Chono Kharaikh. Through the River Toul and the River Dzabkhan, it is connected with the lakes Airag and Khargas. Lake Khar's area is 57.48 km^2. The lake is located at an altitude of 1132 m a.s.l. (Dgebuadze et al., 2014).

Lake Durgen is a closed brackish water lake covering approximately 30 km^2, located south of Lake Khar and connected to it by the channel Khamyn-Kholoy. The lake has a salinity of 4‰. It is one of a group of lakes that were once one large lake, which disappeared about 5000 years ago as a result of a climate change, becoming more arid (Dgebuadze et al., 2014).

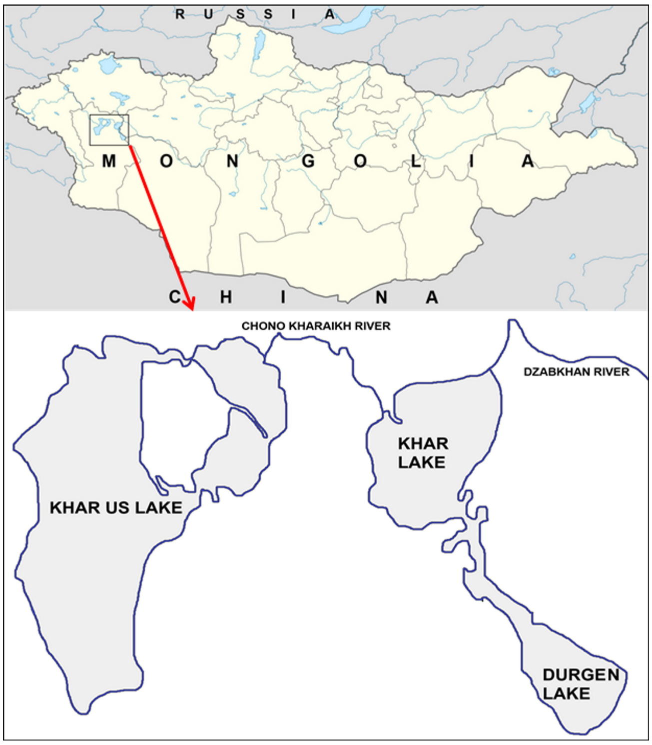

Fig. 1. The location of the Khar Us Nuur National Park and lakes Khar Us, Khar and Durgen in Mongolia.

In total, 52 specimens of *Oreoleuciscus potanini* from three lakes were investigated for their parasite fauna, including 22 ones from Lake Khar, 19 from Lake Us and 11 from Lake Durgen. The fish were caught with fixed gill nets with meshes of 40 mm and 50 mm. The age of *O. potanini* was determined from the opercula (Chugunova, 1959; Pravdin, 1966). The fish diet was investigated using utilising methods according to Borutsky (1974) and Hyslop (1980). The value of particular food items in the diet was calculated by the frequency of occurrence.

The collection, fixation and laboratory processing of parasitological material were carried out according to Bykhovskaya-Pavlovskaya (1985). All fish organs were examined for infection with macroparasites. Mucus for the ectoparasites presence was scraped off the body surface and nasal cavities. Microscopic examination of organs and tissues for Protozoa and Myxosporidia invasion was not conducted. The parasites were identified using several keys (Scarlato, 1985, 1987; Khalil et al., 1994; Moravec, 1994; Sudarikov et al., 2002; Oroš et al., 2010; Pugachev et al., 2010). Methods of identification of *Diplostomum* spp. metacercariae were described by Lebedeva et al. (2020). Parasite data were interrogated and the prevalence (1) and the mean abundance (2) were calculated according to Bush et al. (1997) as follows:

$$E = \frac{N_i}{N} \times 100\% \quad (1),$$

$$M = \frac{\sum n}{N} \quad (2),$$

where E is the prevalence, M is the mean abundance, N is the number of examined fish, N_i is the number of infected fish, and $\sum_n$ is the total number of parasites found in all examined fish.

A systematic list of parasites is given according to the World Register of Marine Species (http://www.marinespecies.org/). Statistical analysis of the infection characteristics and distribution of the parasites was performed using Quantitative Parasitology software (Rózsa et al., 2000; Reiczigel et al., 2019).

Results and Discussion

In Lake Khar, the age of fish from control catches ranged from 4 to 32 years old. Although in this water body, the majority of examined fish was represented by specimens of 4–15 years old, in Lake Khar Us fish were of 8–35 years old. At the same time, the highest number of specimens were assigned to groups of 11 years old, 13 years old, and 16 years old. In Lake Durgen, we noted fish of 4 age groups: 9 +, 10 +, 11 + and 14+. The last two groups prevailed.

In all three investigated water bodies, *O. potanini*'s diet was diverse (Fig. 2), a considerable part being represented by different groups of algae and various insects, including Chironomida larvae. In Lake Durgen, no fish was found in stomachs of the sampled *O. potanini*, although Cladocera crustaceans played a considerable component in their diet.

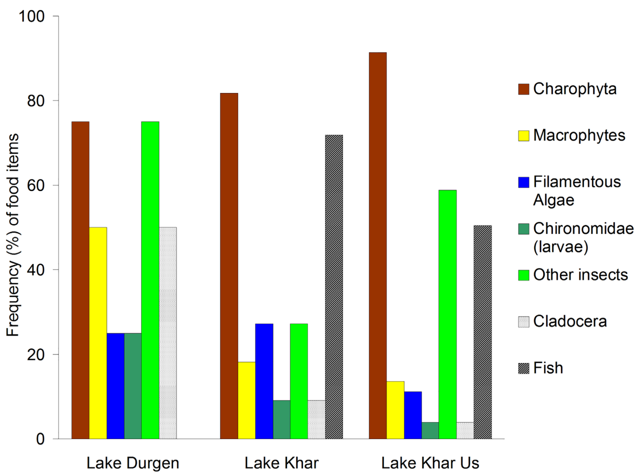

Fig. 2. Diet of *Oreoleuciscus potanini* in the lakes of Khar Us Nuur National Park in 2012.

The age of fish and the diet spectrum are among the main factors determining the parasitic fauna as well as the characteristics and distribution of fish infection. Also invasion levels and parasite species composition in *O. potanini* can vary significantly depending on the biology of the host as well as on the biology of the parasite itself.

Our investigation revealed that *O. potanini* hosted 26 parasite species in three lakes in total (Table 1). All fish examined were infected with parasites. The parasite list was represented by four taxonomic phyla: Acanthocephala (1 species), Annelida (1), Nematoda (4), Platyhelminthes (20). The latter group was the most numerous and diverse, including 3 species of Cestoda, 6 of Monogenea and 11 of Trematoda.

Seven parasite species (monogeneans *Dactylogyrus ersinensis* Spassky & Roytman, 1960, *D. oreoleucisci* Ergens & Dulmaa, 1970, *Gyrodactylus llewellyni* Ergens & Dulmaa, 1967, *G. mongolicus* Ergens & Dulmaa, 1970, *G. oreoleucisci* Ergens & Dulmaa, 1970, *G. pewsowi* Ergens, 1980, and also the leech *Piscicola geometra* (Linnaeus, 1761)) were ectoparasites presented as adults found on skin, fins and gills. Additionally, specimens of *G. oreoleuciscus* were isolated from the nasal cavity of fish. With exception of *G. llewellyni*, all these parasite species were recorded in the three lakes studied. Among the monogeneans *G. oreoleucisci*, *G. mongolicus* and *G. pewzowi* had the highest prevalence and mean abundance. The other species were recorded singularly. The monogeneans are with a direct life cycle without intermediate hosts. *Piscicola geometra* infested quite a lot of fish samples, but the number of parasites was relatively low. According to Pugachev (2004), juvenile *P. geometra* hatching from their cocoons attach onto the surface of the fish in the second half of the summer. So, it is possible that in these lakes the wide distribution of the parasites in *O. potanini* populations is associated with two factors. First of them is collecting the fish during August. The second factor is that in the coastal zone, the feeding of the *O. potanini* with algae and macrophytes provides spatial contact with the leeches.

Another group predominated in the parasite fauna of *O. potanin* consisted of 18 endoparasite species (Table 1). All these parasites have a complex life cycle. Among them nematodes and cestodes are represented in fish by both larval and adult development stages, and Trematoda only by larvae. The majority of endoparasite species was found in the intestine (seven species). Among them, the cestoda *Proteocephalus torulosus* was the most numerous species, sampled in all three lakes. The Acanthocephala *Neoechinorhynchus rutili* (Müller, 1780) and nematode *Rhabdochona humili* Roytman & Trofimenko, 1964 were also found in all three lakes. But their prevalence and mean abundance were low. Four intestine parasites, the nematode *Pseudocapillaria tomentosa* (Dujardin, 1843), cestoda *Caryophyllaeides fennica* (Schneider, 1902) and trematodes *Allocreadium isoporum* (Looss, 1894) and *A. transversale* (Rudolphi, 1802) infected fish in the lakes Khar and Khar Us only (Table 1). *Allocreadium isoporum* (Looss, 1894) was the most numerous species among them.

The majority of these parasites enter *O. potanini*, while the fish are feeding on invertebrates, in which the parasites are present. A considerable number of invertebrates inhabited the water bodies of the Great Lakes Depression (Krylov, 2013; Krylov et al., 2018; Prokin, 2018). The presence of *Neoechinorhynchus rutile* reflects the fish feeding by ostracods and amphipods as intermediate hosts for helminthes. A low prevalence and mean abundance indicated a low consumption by fish of ostracods and amphipods. The life cycle of *Pseudocapillaria tomentosa* as well as for *Caryophyllaeides fennica* is not exactly known. But most likely the fish is infected by them by feeding on oligochaetes (Khalil et al., 1994; Moravec, 1994). In the River Dzabkhan system, 12 species of oligochaetes have been identified (Dgebuadze et al., 2014; Prokin, 2018). The life cycle of *Rhabdohona humili* has not been studied, either. However, the parasites likely enter the fish body while feeding on Ephemeroptera (Pugachev, 2004).

Another species of cestode, *Proteocephalus torulosus*, was the most numerous and widespread among the cestodes on *O. potanini* in the three studied lakes. The development cycle of the Cestoda includes two obligate hosts, including Copepoda as the intermediate hosts and the fish as final hosts (Khalil et al., 1994). The age structure of the helminth populations and morphological characteristics of *P. torulosus* from Mongolian fish have been studied extensively (Anikieva et al., 1987, 2013; Anikieva, 2004). As a result, it was shown that the morphological variability of the reproductive group of *P. torulosus* is comparable with the high level and range of variability of the adult and mature parasite group from *O. potanini*. Assessment of the intrapopulation diversity of *P. torulosus* and its structure showed that the immature helminth group does not significantly differ from the mature one from *O. potanini* in Lake Nogon (Anikieva et al., 2013). In the water bodies of Mongolia, *O. potanini* is the only final host for *P. torulosus*. But the latter species is a widespread parasite of many Cyprinidae species in the Holarctic (Anikieva et al., 1987; Pugachev, 2002; Anikieva, 2004).

The findings of *Allocreadium isoporum* and *A. transversale* confirmed the predominance of benthos in the fish diet, since either amphipods or aquatic insect larvae serve as intermediate hosts of parasites. In Mongolia, *A. transversale* was revealed in *Rutilus rutilus* and *Thymallus brevirostris*, too. In total, five *Allocreadium* species were recorded in fish in Mongolia (Pugachev, 2003; Lebedeva et al., 2015). *Allocreadium isoporum* is a widespread parasite of Cyprinidae fish (Petkevičiūtė et al., 2010). The status and biology of *A. transversale*, as well as its distribution, need further research. So far, it is believed that the latter species is confined to the genera *Misgurnus*, *Rhynchocypris* and *Phoxinus* (Pugachev, 2004).

Another Nematoda species, *Philometra oreoleucisci* Moravec & Ergens, 1970, was one of the numerous parasites of *O. potanini* found exclusively in the caudal fin of the fish. The nematodes were revealed in all three studied lakes, but their abundance was higher in the lakes Khar and Khar Us (Table 1). The life cycle of *Ph. oreoleucisci* has not been studied. But copepods are most likely the first intermediate hosts, as for other *Philometra* species (Moravec, 1994). It is possible that a future study of Copepoda in terms of parasites noted in the water bodies of the Great Lakes Depression (Krylov, 2013; Krylov et al., 2018) will clarify this issue.

Eleven helminth species parasitised fish on larval stages in the body cavity, cranial cavity and eyes. In the body cavity, we found nematodes *Contracaecum* sp., cestode *Dibothriocephalus dendriticus* Nitzsch, 1824 and trematode *Hysteromorpha triloba* (Rudolphi, 1819). Single plerocercoids *D. dendriticus* were found in the lakes Khar and Khar Us only (Table 1). Larvae of *Contracaecum* sp. and *Hysteromorpha triloba* metacercariae had both a high prevalence and mean abundance in fish in all three lakes. The first intermediate hosts of *D. dendriticus* are copepods (Pugachev, 2002). Fish get infected by eating infected invertebrates. According by the infection rates, the proportion of Crustacea is very small in the diet. And our data on diet spectrum of *O. potaninin* have confirmed this.

Table. List of parasites of *Oreoleuciscus potanini* and fish infection rates in the three lakes of Khar Us Nuur National Park

Parasite species	Lake Khar (n = 22)			Lake Khar Us (n = 19)			Lake Durgen (n = 11)		
	E	M	min–max	E	M	min–max	E	M	min–max
Phylum Acanthocephala									
Class Eoacanthocephala									
Neoechinorhynchus rutili (Müller, 1780)	27	0.4 (0.14–0.82)	1–3	26	0.37 (0.11–0.63)	1–2	9	0.09 (0.00–0.27)	(1)
Phylum Annelida									
Class Clitellata									
Piscicola geometra (Linnaeus, 1761)	64	1.1 (0.64–1.55)	1–4	58	1.3 (0.7–2.0)	1–5	–	–	–
Phylum Nematoda									
Class Enoplea									
Pseudocapillaria tomentosa (Dujardin, 1843)	14	0.7 (0.14–1.90)	3–8	11	0.16 (0.00–0.47)	1–2	–	–	–
Class Chromadorea									
Contracaecum sp., l	100	7.18 (2.0–28.2)	1–106	100	6.21 (5.16–7.47)	3–12	73	1.3 (0.7–1.9)	1–3
Philometra oreoleucisci Moravec & Ergens, 1970	80	4.2 (2.82–5.77)	1–13	75	3.6 (2.32–5.29)	1–12	100	9.2 (7.45–11.60)	4–18
Rhabdochona humili Roytman & Trofimenko, 1964	32	1.27 (0.55–2.54)	1–8	47	1.6 (0.74–2.95)	1–8	45	0.64 (0.18–1.09)	1–2
Phylum Platyhelminthes									
Class Cestoda									
Caryophyllaeides fennica (Schneider, 1902)	14	0.23 (0.00–0.55)	1–2	26	0.4 (0.16–0.89)	1–3	–	–	–
Dibothriocephalus dendriticus Nitzsch 1824, pl	14	0.14 (0.00–0.27)	1–1	21	0.21 (0.00–0.37)	1–1	–	–	–
Proteocephalus torulosus (Batsch, 1786)	55	6.6 (2.14–17.90)	1–55	74	2.6 (1.47–4.36)	1–11	55	1.4 (0.54–2.30)	1–5
Class Monogenea									
Dactylogyrus ersinensis Spassky & Roytman, 1960	17	0.2 (0.05–0.32)	1–1	11	0.1 (0.00–0.22)	1–1	9	0.01 (0.00–0.27)	(1)
Dactylogyrus oreoleucisci Ergens & Dulmaa, 1970	13	0.18 (0.00–0.41)	1–2	5	0.16 (0.00–0.47)	(3)	9	0.01 (0.00–0.27)	(1)
Gyrodactylus llewellyni Ergens & Dulmaa, 1967	8	0.14 (0.00–0.36)	1–2	5	0.05 (0.00–0.16)	(1)	–	–	–
Gyrodactylus mongolicus Ergens & Dulmaa, 1970	75	4.5 (3.01–5.95)	2–13	42	1.16 (0.47–2.47)	1–3	27	0.4 (0.09–0.54)	1–1
Gyrodactylus oreoleuciscus Ergens & Dulmaa, 1970	88	4.7 (3.14–6.64)	1–15	79	2.9 (1.47–4.47)	1–12	64	1.4 (0.64–2.00)	1–3
Gyrodactylus pewzowi Ergens, 1980	80	2.4 (1.73–3.14)	1–7	95	1.3 (1.00–1.63)	1–3	82	1.2 (0.64–1.64)	1–2
Class Trematoda									
Allocreadium isoporum (Looss, 1894)	59	5.1 (2.33–10.50)	3–32	58	4.94 (2.89–7.63)	4–16	–	–	–
Allocreadium transversale (Rudolphi, 1802)	18	0.5 (0.09–1.27)	1–5	5	0.1 (0.00–0.32)	(2)	–	–	–
Diplostomum pseudospathaceum Niewiadomska, 1984, mtc	50	1.8 (1.04–2.91)	2–8	47	0.95 (0.42–1.68)	1–5	–	–	–
Diplostomum spathaceum (Rudolphi, 1819), mtc	73	2.7 (1.68–4.09)	1–11	68	1 (0.58–1.47)	1–3	100	3.6 (2.45–4.64)	1–7
Diplostomum sp. LIN2 Blasco-Costa, Faltynkova, Georgieva, Skirnisson, Scholz, Kostadinova, 2014, mtc	9	0.3 (0.00–1.09)	2–5	21	0.8 (0.21–1.84)	2–6	–	–	–
Hysteromorpha triloba (Rudolphi, 1819), mtc	67	51 (28.1–81.8)	1–170	79	46 (31.1–60.70)	22–113	100	10 (6.82–12.1)	1–17
Ichthyocotylurus pileatus (Rudolphi, 1802), mtc	64	5.6 (3.55–8.30)	2–17	47	4.3 (2.11–7.84)	4–23	82	4.7 (2.64–7.45)	1–13
Ornithodiplostomum scardinii (Shulman in Dubinin, 1952), mtc	14	0.14 (0.00–0.27)	1–1	11	0.16 (0.00–0.43)	1–2	9	0.01 (0.00–0.27)	(1)
Posthodiplostomum brevicaudatum (Nordmann, 1832), mtc	23	1.14 (0.32–2.59)	1–9	16	0.16 (0.00–0.32)	1–1	9	0.01 (0.00–0.27)	(1)
Tylodelphys cerebralis (Chakrabarti, 1968), mtc	5	0.09 (0.00–0.23)	1–1	11	0.05 (0.00–0.32)	(2)	9	0.01 (0.00–0.27)	(1)
Tylodelphys clavata (Nordmann, 1832), mtc	18	0.27 (0.05–0.55)	1–2	11	0.11 (0.00–0.26)	1–1	9	0.01 (0.00–0.27)	(1)
Total parasite species	26			26			15		

Note: n – number of fish dissected; E – prevalence (%); M – mean abundance; l – larva; pl – plerocercoid; mtc – metacercaria. In brackets – 95% confidential limits for the population mean abundance by the BCa method with 2000 bootstrap replications (Reiczigel et al., 2019).

The first intermediate hosts of *Contracaecum* sp. are numerous invertebrate species, e.g. copepods and larvae of dragonflies, and dipterans (Moravec, 1994). A considerable number of various invertebrates resides in the River Dzabkhan basin (Krylov et al., 2018; Prokin, 2018). Larvae of *Contracaecum* spp. are very difficult for identification according to morphology before the third development stage (Moravec, 1994). Probably three *Contracaecum* species (*Contracaecum rudolphii* Hartwich, 1964, *C. microcephalum* (Rudolphi, 1809), *C. spasskii* Mozgovoi, 1950) can parasitise on *O. potanini* as well as on other fish species in the Great Lakes Depression. We found adult nematodes *C. rudolphii* and *C. microcephalum* in *Phalacrocorax carbo sinensis* Shaw & Nodder, 1801 and *Larus argentatus mongolicus* Suschkin, 1925 on the Khar Lake shore, respectively (Lebedeva & Chantuu, 2015). In addition, we observed third stage larvae of *C. microcephalum* in *Barbatula conilobus* in the River Dzabkhan (Lebedeva et al., 2019). Additionally, the finding of nematodes *C. rudolphii* and *C. spasskii* in birds in China increases the likelihood to reveal these species in Mongolia (Li et al., 2013).

Snails of the genus *Gyraulus* are the first intermediate hosts for the trematode *Hysteromorpha triloba*. After leaving the snails, cercariae actively penetrate into the fish skin and then move to the body cavity. This species parasitises in different fish not only in the Holarctic, but also in the Neotropical region, by ending the development only in the specific host *Phalacrocorax carbo* (Locke et al., 2011; Sereno-Uribe et al., 2018a). Adults of *H. triloba* were previously founded in *Ph. carbo* from the Khar Lake shore (Lebedeva & Chantuu, 2015).

Metacercariae of *Ichthyocotylurus pileatus* (Rudolphi, 1802) were present in a large number in the body cavity of *O. potanini* sampled in all three lakes (Table 1). In addition, several parasites were found in eyes retina of fishes. To date, various development stages of *I. pileatus* have been identified using molecular methods in Canada, Great Britain and the Czech Republic (Bell et al., 2001; Locke et al., 2010; Heneberg et al., 2018). The first intermediate hosts of the parasite are *Valvata* spp. snails, while the final hosts are fish-eating birds. It is believed that *Ichthyocotylurus pileatus* is a parasite of Coregonidae and Percidae fish (Niewiadomska, 2001). However, in the water bodies of the Great Lakes Depression, *O. potanini*, as the dominating fish species, assumes the role of an intermediate host.

Five Trematoda species were isolated from the eyes of *O. potanini*. There were three species in the lens: *Diplostomum spathaceum* (Rudolphi, 1819), *D. pseudospathaceum* Niewiadomska, 1984 and *Diplostomum* sp. LIN2 Blasco-Costa, Faltynkova, Georgieva, Skirnisson, Scholz, Kostadinova, 2014. All parasite species invaded the fish with active swimming cercariae. Metacercariae of *Diplostomum spathaceum* were very numerous in all three water bodies. It seems that *D. spathaceum* is widespread in the whole of Mongolia. Metacercariae of the species were also found in the eye lenses of *Thymallus brevirostris* in water bodies of the River Dzabkhan basin. Additionally, *Rutilus rultulus* from Lake Terkhiin Tsagaan (Arctic Ocean basin) was infected by this trematode. Adults of *D. spathaceum* were found in intestine of *Larus argentatus* (Lebedeva & Chantuu, 2015; Lebedeva et al., 2015, 2020). Two other representatives of the genus were *D. pseudospathaceum* and *Diplostomum* sp. LIN2. They were less numerous in fish from the lakes Khar and Khar Us only. *Diplostomum pseudospathaceum* seems to have the same list of hosts as *D. spathaceum* (Pérez-del-Olmo et al., 2014; Locke et al., 2015; Hoogendoorn et al., 2020). The host range and geographical distribution of *Diplostomum* sp. LIN2 requires further study, because the metacercaria have been found only in distinct Iceland and Mongolia (Blasco-Costa et al., 2014; Faltýnková et al., 2014; Lebedeva et al., 2020).

Few metacercariae of *Posthodiplostomum brevicaudatum* (Nordmann, 1832) and *Tylodelphys clavata* (Nordmann, 1832) were isolated from vitreous humor of fish eyes in the three lakes investigated. Both parasites invaded the fish with active swimming cercariae. The first intermediate hosts for *P. brevicaudatum* are the snails *Planorbis planorbis* (Linnaeus, 1758) and *P. carinatus* Müller, 1774, and the final hosts are fish-eating birds like *Ardea* spp. and *Sterna* spp. (Sudarikov et al., 2002). For *Tylodelphys clavata*, the first intermediate hosts were snails of the genus *Lymnaea* and the final ones are several fish-eating bird species (Sudarikov et al., 2002).

In the cranial cavity of *O. potanini*, two species, *Ornithodiplostomum scardinii* (Shulman in Dubinin, 1952) and *Tylodelphys cerebralis* (Chakrabarti, 1968), were observed. Few metacercariae of both species parasitise fish in the lakes Khar and Khar Us. According to Chaudhary et al. (2017), metacercariae of *T. cerebralis* could be localised not only in the cranial cavity but also in the vitreous humor of eyes. The diplostomoid larvae, including the genus *Tylodelphys*, are morphologically very similar. Also some new species of the genus *Tylo-*

delphys have been isolated from new hosts in different parts of the world in recent years (Sokolov et al., 2013; Otachi et al., 2015; Chaudhary et al., 2017; Sereno-Uribe et al., 2018b). Therefore, it is necessary to conduct further investigations (preferably using molecular methods) on fish metacercariae in Mongolia. The adult trematodes of both genera are parasites of piscivorous birds, like *Ardea* spp. and *Sterna* spp. (Sudarikov et al., 2002; Sitko & Rzad, 2014; Stoyanov et al., 2017).

The high diversity of parasites completing their development in birds as well as high invasion rates of *O. potanini* in the studied lakes are most likely associated with the wide distribution and increasing in number of fish-eating birds in the Khar Us Nuur National Park (Zvonov et al., 2016). On the other hand, fish feeding with algae and macrophytes provides spatial contact with the cercariae escaping the snails and increases the infection of fish with trematodes. A high abundance of parasites (*Contracaecum microcephalum*, *C. rudolphii*, *Dibothriocephalus dendriticus*, *Hysteromorpha triloba*, *Diplostomum spathaceum*, *D. pseudospathaceum*) was found in bird intestine on the Khar Lake shore that evidences that fish take significant part of birds' diet.

Among 26 parasites revealed in *O. potanini*, only five species were the most specific for this host (monogeneans *Gyrodactylus mongolicus*, *G. oreoleucisci*, *G. pewsowi* and nematodes *Philometra oreoleucisci*, *Rhabdochona humili*). These parasites were described from *Oreoleusiscus potanini* only as well as the geographic range of these species is limited to the water bodies of Western Mongolia (Pugachev, 2002). Monogeneans *Gyrodactylus llewellyni*, *Dactylogyrus ersinensis* and *D. oreoleucisci* were firstly revealed as parasites of *Oreoleuciscus* species only. But later species of *Phoxinus* and *Rhynchocypris* were found to be hosts for the parasites (Pugachev, 2002). It seems that these species are more common with fish in the Asian part of the Palaearctic.

The 21 species found are parasites of different fish with wide geographical range. Species as *Neoechinorhynchus rutile, Caryophyllaeides fennica* and *Pseudocapillaria tomentosa* are widespread in the Holarctic. They are parasites of various freshwater fish, mainly Cyprinidae (Pugachev, 2002, 2004). *Ichthyocotylurus pileatus* also have been identified in different parts of the Holarctic (Bell et al., 2001; Locke et al., 2010; Heneberg et al., 2018). In water bodies of Mongolia, *O. potanini* is the only final host for *Proteocephalus torulosus*. But in general, *P. torulosus* is a widespread parasite of Cyprinidae fish in the Holarctic (Anikieva et al., 1987; Pugachev, 2002; Anikieva, 2004). The trematodes *Diplostomum* spp., *Posthodiplostomum brevicaudatum*, *Ornithodiplostomum scardinii*, and *Tylodelphys clavata* are common in the Palearctic waters (Locke et al., 2015; Stoyanov et al., 2017; Hoogendoorn et al., 2020). *Allocreadium isoporum* is a widespread parasite of Cyprinidae fish in the Palearctic (Petkevičiūtė et al., 2010), while the status and biology of *Allocreadium transversale*, as well as its distribution, need further research. *Piscicola geometra* is a parasite of many fish species in water bodies of the Northern Hemisphere (Pugachev, 2004).

In general, comparison of the parasite species composition of fish between the three studied water bodies showed the depletion of the latter in Lake Durgen. In this water body, *O. potanini* had only 15 parasite species, while there were no parasites associated with other hosts except of *O. potanini* (Table 1). The infection intensity of these parasites were also low in the lakes Khar and Khar Us. It is likely that, despite the ability of fish to exist in conditions of higher salinity (Mironovsky et al., 2019), parasites have not managed to adapt to these conditions. Alternatively, another possible reason for the absence of these parasites in Lake Durgun is a decrease of invertebrates in the biomass. This in its turn is determined by two factors, including the deterioration of the hydrodynamic conditions due to a decrease in water level and an increase in the load from the catchment due to the Durgun reservoir creation (Krylov, 2013). By analysing the parasite species composition of *O. potanini* in the Great Lakes Depression, we can assume that it has not changed considerably since the 1980s (Kazakov & Paranlejamts, 1985; Paranlejamts, 1993; Roitman et al., 1997; Pugachev, 2002, 2003, 2004). Earlier, 32 helminth species were identified in the Great Lakes Depression basin (Roitman et al., 1997; Pugachev, 2002, 2003, 2004). According to Roitman et al. (1997), in Lake Durgen, the number of species was also lower than in the lakes Khar and Khar Us. However, specific parasites as *Gyrodactylus mongolicus* and *G. oreoleucisci* were not recorded in the Lake Durgen. In our study, the rare nematode *Eustrongylides mergorum* (Rudolphi, 1809) was not recorded. In addition, we have not found the cestode *Paradilepis scolecina* (Rudolphi, 1819) in *O. potanini*. Previously, both parasites were detected in this host species from different water bodies of Mongolia (Pugachev, 2002).

But adult *Paradilepis scolecina* were revealed in intestine of *Phalacrocorax carbo* in the Khar Lake shore (Lebedeva & Chantuu, 2015). Alternatively, it is possibly associated with the small fish sampling compared with previous studies (e.g. Kazakov & Paranlejamts, 1985; Paranlejamts, 1993; Roitman et al., 1997; Pugachev, 2002, 2003, 2004). Moreover, fluctuations of fish infection rates by year are possible. For example, in 2011, the infection of *O. potanini* by *Proteocephalus torulosus* in Lake Har-Nuur amounted to 13% (two specimens of 15 fish examined), under infection rate of 18 and 40 specimens, and abundance index of 3.9 specimens (Anikieva et al., 2013). This is several times lower than in our study (Table 1).

But some differences in the species list could be associated with taxonomic renaming and the development of the phylogeny of certain parasite groups, e.g. for the trematodes *Diplostomum* spp. According to previously published data, *O. potanini* is a host for nine species of diplostomids (Roitman et al., 1997; Pugachev, 2003; Batueva, 2011). A comprehensive study of *O. potanini* metacercaria from different locations in the Central Asian Inland Basin showed the presence of three species only named as *D. pseudospathaceum*, *D. spathaceum* and *Diplostomum* sp. LIN2. In Mongolian water bodies, a total of five *Diplostomum* species were found. Additionally *Diplostomum baeri* Dubois, 1937 was revealed in *Perca fluviatilis* and *D. mergi* Dubois, 1932 in *Barbatula conilobus* from Lake Terkhiin Tsagaan and River Dzabkhan, respectively (Lebedeva et al., 2015, 2020). Further investigation of *O. potanini* could identify new diplostomids. Similarly, recent studies of cestodes from the Diphyllobothriidae attributed representatives of *Diphyllobothrium dendriticum* (Nitzsch, 1824) to *Dibothriocephalus dendriticus* (Waeschenbach et al., 2017).

Oreoleuciscus species form an endemic fish group in Central Asia, belonging to the Cyprinidae. According to paleontological data, this is a relatively young group. Fossil records of ancestral oreoleuciscoid forms date back to the border between the Pliocene and Pleistocene. In particular, on the basis of the analysis of the nucleotide sequence polymorphism of the mitochondrial DNA, it was established that the close relatives of *O. potanini* are phoxinine fish belonging to the genera *Phoxinus*, *Rhynchocypris*, *Tribolodon*, and *Pseudoaspius*. Moreover, the closest relationships were discovered between *Oreoleuciscus potanini* and *Rhynchocypris*. *lagowskii* (Dybowski, 1869) (Slynko & Borovikova, 2012; Kartavtsev et al., 2017; Sakai et al., 2020). In Western Mongolia, *Oreoleuciscus potanini* resides in various water bodies, including fresh and brackish-water lakes, streams, rivers, located at altitudes of 700–2500 m a.s.l. The noncompetitive evolution of a relatively young group developing in a region with exceptionally variable environmental conditions (Sokolov & Shatunovsky, 1983) led to its extremely high morphological diversity and genetic heterogeneity (Slynko & Dgebuadze, 2009).

Data on the parasite fauna of *O. potanini* confirmed the evolutionary youth of this fish group. Some of the parasites found are considered to be endemics and specific parasites found only in *Oreoleuciscus* spp. (*Gyrodactylus mongolicus*, *G. oreoleucisci*, *G. pewsowi*, *Philometra oreoleucisci*, *Rhabdochona humili*). The formation of these species as valid ones occurred probably after *Oreoleuciscus* diverged from the other Leuciscinae fishes (Roitman et al., 1997). Some parasites were noted in *O. potanini* as well as in the phylogenetically closest fish of the genera *Phoxinus* and *Rhynchocypris*. So, the monogeneans *Gyrodactylus llewellyni*, *Dactylogyrus ersinensis* and *D. oreoleucisci* indicate a phylogenetic relationship between these host species in the Central Asian Inland Basin and western Mongolia. Pugachev (2001) reported on the same situation with the parasite *Myxobolus mongolicus* Pronin, 1973. It was previously considered to be an endemic of the West Mongolian Province as a specific parasite of *O. potanini*. But later it was found in *Thymallus brevirostris* and *Rhynchocypris percnurus* from the River Lena and River Selenga, as well as in the Far East. Parasites are evolved in parallel with their hosts. The complementary adaptations of parasites and their hosts are formed over a long co-evolution (Bykhovsky, 1957). These data were obtained using molecular methods for many monogeneas (e.g. Ziętara & Lumme, 2003; Vanhove et al., 2014; Lumme et al., 2017). In our materials, an example is the invasion of *O. potanini* with all specific parasites in oligotrophic brackish-water of Lake Durgen, while some of the non-specific ones were absent in the lake's fish parasite fauna (Table 1). Additionally, some helminthes (*Caryophyllaeides fennica*, *Proteocephalus torulosus*) parasitise on different fish species, but mainly on Cyprinidae. In Mongolia, they parasitise only on *O. potanini*. The high morphological variability of *P. torulosus* on *Oreoleuciscus potanini* confirmed the adaptation of the parasite and the host to extremely variable environmental conditions of the region as co-evolution (Anikieva et al., 1987, 2013). The other group includes many widespread parasite species such as *Diplostomum* spp., *Ichthyocotylurus pileatus*, *Tylodelphys* spp., *Hysteromorpha triloba*, *Allocreadium* spp., and *Contracaecum* spp.. Perhaps due to adaptation to the only host *O. potanini*, these helminthes have being in the process of micro evolution and eventually the formation of new species. Therefore, since parasites co-evolve with hosts, information on their species composition can be useful in addressing the systematics of *Oreoleuciscus* fish, any changes in their biology, and can also help in the study of ecosystem dynamics as a whole.

Conclusions

It could be assumed that the current situation with the *Oreoleuciscus* spp. divergence and their spreading was formed in the Pleistocene, in the Chibanian period (Sytchevskaya, 1989). So, a part of their parasite fauna including endemics was formed at the same time before the fish divergence from the ancestral form. The absence of considerable long-term changes in the parasite composition indicates that the ecosystem of water bodies in the Khar Us Nuur National Park is in sufficient balance, where parasites are an integral biodiversity component. The fauna of this Protected Area is diverse. It presents a variety of organism groups involved in the development of parasites at different stages.

However, discussion of the parasite fauna richness of *O. potanini* requires further investigation to compare the species composition of hosts from various water bodies. Additionally, studies based on molecular genetics of the parasites taxonomy are required to allow re-descriptions of species morphology. Consequently, further study needs to concentrate the attention on these two points to collect data on the species composition of both parasites and hosts. In addition, parasite taxonomy is developing, requiring molecular studies and re-descriptions of species morphology.

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ПАРАЗИТЫ *OREOLEUCISCUS POTANINI* (CYPRINIDAE) В ОЗЕРАХ НАЦИОНАЛЬНОГО ПАРКА ХАР-УС-НУУР (МОНГОЛИЯ)

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Пресноводные экосистемы Монголии принадлежат к трем основным центральноазиатским водным бассейнам: Арктический бассейн, бассейн реки Амур и Центральноазиатский внутренний бассейн. Значительную часть последнего занимает Котловина Больших озер. Один из немногих живущих там видов рыб, *Oreoleuciscus potanini*, является наиболее широко распространенным эндемическим видом в Центральноазиатском регионе. Изучение паразитов *O. potanini* в Котловине Больших озер не являются регулярными в последние годы. Поэтому данное исследование было проведено с целью изучения видового разнообразия паразитов гельминтов *O. potanini* на трех озерах национального парка «Хар-Ус-Нуур». Всего в августе 2012 г. на озерах Хар, Хар-Ус и Дурген было собрано 52 экземпляра *O. potanini*. Помимо паразитофауны были изучены возраст и спектр питания хозяев. Рыбы были исследованы на заражение экто- и эндо-макропаразитами. Видовой состав метацеркарий трематод *Diplostomum* spp. из глаз рыб исследован с помощью молекулярных методов. В озерах Хар и Хар-Ус возраст рыб варьировал от 4 до 32 лет и от 8 до 35 лет, соответственно. В оз. Дурген исследованы рыбы четырех возрастных групп (9, 10, 11 и 14 лет). Во всех трех озерах основной пищей *O. potanini* служили водоросли и различные насекомые, в том числе личинки семейства Chironomidae. При исследовании питания мы обнаружили, что в озере Дурген важным компонентом рациона питания рыб были ракообразные Cladocera. Рыбы среди объектов питания *O. potanini* в этом водоеме не отмечены. Всего в ходе исследования было выявлено 26 видов паразитов в трех озерах. Общая фауна представлена четырьмя типами, включая Acanthocephala (один вид), Annelida (один вид), Nematoda (четыре вида), Platyhelminthes (двадцать видов). Последняя группа была наиболее многочисленной и разнообразной, включая три вида Cestoda, шесть видов Monogenea и 11 видов Trematoda. Пять видов паразитов были специфичны только для *O. potanini* (моногенеи *Gyrodactylus mongolicus*, *G. oreleucisci*, *G. pewsowi*, нематоды *Philometra oreoleucisci* и *Rhabdochona humili*). Остальные гельминты демонстрировали низкую специфичность хозяев, так как паразитируют у широкого круга рыб в Голарктике. В фауне паразитов преобладают личинки эндогельминтов. Большинство этих паразитов проникают в рыбу через различные виды беспозвоночных во время питания ими *O. potanini*. Наше исследование выявило новые данные о видовом разнообразии метацеркарий *Diplostomum* spp. в глазах *O. potanini*. Они представлены тремя видами: *Diplostomum spathaceum*, *D. pseudospathaceum* и *Diplostomum* sp. LIN2. Видовое богатство и разнообразие паразитов было значительно выше для *O. potanini* из озер Хар и Хар-Ус (26 видов), чем для *O. potanini* в оз. Дурген (15 видов). Возможной причиной отсутствия некоторых паразитов в последнем водоеме является повышенная соленость воды. Несмотря на то, что рыба может существовать в условиях повышенной солености, вероятно, паразиты (или их беспозвоночные хозяева) не приспособлены к ней. Наши исследования позволили уточнить видовой состав паразитов в озерах национального парка Хар-Ус-Нуур, в том числе охарактеризованы уникальные сообщества паразитов в экосистемах Котловины Больших озер. Результаты исследований паразитофауны *O. potanini* подтверждают сведения об эволюционной молодости группы рыб рода *Oreoleuciscus*.

Ключевые слова: бассейн, видовой состав, гельминт, Котловина Больших озер, река Дзабхан, рыбы, эндемик